Bulletin of Entomological Research (2004) **94**, 123–136 DOI: 10.1079/BER2004287

An aerial netting study of insects migrating at high altitude over England

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Abstract

Day and night sampling of windborne arthropods at a height of 200 m above ground was undertaken at Cardington, Bedfordshire, UK, during July 1999, 2000 and 2002, using a net supported by a tethered balloon. The results from this study are compared with those from the classic aerial sampling programmes carried out by Hardy, Freeman and colleagues over the UK and North Sea in the 1930s. In the present study, aerial netting was undertaken at night as well as daytime, and so the diel periodicity of migration could be investigated, and comparisons made with the results from Lewis and Taylor's extensive survey of flight periodicity near ground level. In some taxa with day-time emigration, quite large populations could continue in high-altitude flight after dark, perhaps to a previously underrated extent, and this would greatly increase their potential migratory range. Any trend towards increases in night temperatures, associated with global warming, would facilitate movements of this type in the UK. Observations on the windborne migration of a variety of species, particularly those of economic significance or of radar-detectable size, are briefly discussed.

Introduction

In many insect species the study of migration is key to a proper understanding of population dynamics and gene-flow, and to the evolution of various associated behavioural, physiological and life-history traits (Drake & Gatehouse, 1995; Dingle, 1996, 2001; Gatehouse, 1997; Denno *et al.*, 2001; Mallet, 2001; Woiwod *et al.*, 2001; Osborne *et al.*, 2002). In addition, migration studies have led to many practical applications, for example, in forecasting outbreaks of migratory pests (Pedgley, 1993; Drake & Gatehouse, 1995), assessing the effects of habitat fragmentation for the conservation of threatened species (Hanski & Gilpin, 1991; Wilson & Thomas, 2002), and in evaluating the effects of global environmental change on the abundance, phenology or biodiversity of insect communities (Woiwod & Harrington, 1994; Parmesan, 2001).

Most insect migrants take advantage of the wind to travel much further than would be achievable by their powered flight alone. They ascend above their 'flight boundary layer' (Taylor, 1974), frequently to altitudes of several hundred metres above the ground, where they can utilize fast-moving airstreams to travel tens or hundreds of kilometres in a single flight (Drake & Gatehouse, 1995; Woiwod *et al.*, 2001; Chapman *et al.*, 2003). However, high-altitude flight, together with the relatively small body size of insects, and the fact that many species are nocturnal, means that it is intrinsically difficult to observe and quantify their movements whilst they are in progress. Consequently, many studies of insect migration have relied upon indirect evidence from ground-level trapping systems, but these methods do not provide

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information on the migrants' height of flight. Knowledge of this is essential for ascertaining the airstreams in which migrants are actually flying, and thus their likely flight-paths and source areas (Chapman *et al.*, 2002).

The only technique suitable for long-term, automatic monitoring of insect migration over a wide range of altitudes is vertical-looking radar (VLR), which can provide information on the size, shape, wing-beat frequency, displacement vectors and orientation of migrating insects from heights over a vertical range of ~ 1 km (Smith *et al.*, 2000; Drake *et al.*, 2001; Chapman *et al.*, 2002, 2004). In certain circumstances, such as the mass migration of an insect species with characteristic radar scattering properties, it is possible to determine the identity of radar-detected insect targets from the shape and size data embedded in the returned signals (Chapman *et al.*, 2002). However, in the UK the airborne insect fauna is not generally dominated by overflights of a single species, and thus it is highly desirable to have supplementary data from direct trapping methods to facilitate the identification of radar targets. In addition, aerial trapping is still the only way to determine the composition of the insect fauna which is too small (< 1 mg) to be detectable with currently-used insect monitoring radars.

High-flying migrant insects have been sampled with nets suspended from tethered aerodynamically-shaped balloons (blimps), kites or aircraft (both manned and remotely-piloted) (Reynolds *et al.*, 1997). During the 1930s, extensive daytime sampling of airborne migrants was carried out at heights of 50–600 m above the UK, and the most abundant day-flying species were documented (Hardy & Milne, 1938; Freeman, 1945). Further sampling was carried out in the 1940s and 1950s at heights of up to 610 m over Bedfordshire, southern England by C.G. Johnson and colleagues (Johnson *et al.*, 1962; Johnson, 1969), but their studies concentrated on a few groups (e.g. aphids, frit flies) and the taxonomic composition of their high-altitude catches were not published in any detail. While more recent high-altitude sampling has been conducted in various other parts of the world, e.g. China (Riley *et al.*, 1991, 1994, 1995b), India (Riley *et al.*, 1995a; Reynolds *et al.*, 1999), Australia (Farrow & Dowse, 1984; Drake & Farrow, 1985), the USA (Isard *et al.*, 1990; Greenstone *et al.*, 1991) and the Canary Islands (Ashmole & Ashmole, 1988), work in the UK has not continued. Thus there is a paucity of current information about the airborne insect fauna over the UK (and, for that matter, over Europe generally) and in particular, the taxonomic composition of high-flying nocturnal migrants has never been documented. To help remedy this situation, the results of three periods of intensive day and night trapping, using a balloon-supported net, over southern England, are reported here.

Materials and methods

Aerial netting was carried out at ~ 200 m above ground at Cardington Airfield, Bedfordshire, UK (52°06′N, 0°25′W), where the flying of tethered balloons above the normal Civil Aviation Authority limit of 60 m is permitted because of an official aircraft exclusion zone (Danger Area EGD206). (Incidentally, this was also the site where Johnson and colleagues carried out their aerial netting studies in the 1950s). Cardington is about 30 km north of the VLR site at Rothamsted Research, Harpenden, Hertfordshire, but given the spatially random nature of aerial insect populations (Taylor, 1974) one can assume that the samples were reasonably representative of the insect fauna detected by the radar at Rothamsted. Aerial netting was carried out during periods of three to four weeks duration during July 1999, 2000 and 2002. Sampling was semi-continuous throughout the day and night, whenever weather conditions permitted balloon flying (i.e. there was a low risk of rain or lightning), and the wind was strong enough to allow sampling (>3 m s^{-1}, as below this the net will not sample efficiently). As required by CAP393 Air Navigation regulations, marker pennants were tied to the tethering line during day flights, and white and red lights were attached to the balloon at night. Approximate sampling periods (in BST) were as follows: morning (10.00–14:00), afternoon (14:00–18:00), dusk (21:00–22:00) and night-time (22:00–05:00).

Sampling procedures were generally similar to those of Riley *et al.* (1991, 1995a). Insects were caught in a tapering net suspended several metres below an aerodynamically shaped, helium-filled balloon (blimp) attached to a lightweight motorized winch. The blimp (Advanced Inflatable Products Ltd, Southend-on-Sea, UK) was 12.5 m^3 in volume, and consisted of a single gas envelope of polyurethane-coated nylon fabric with a gas expansion chamber at the rear. The net, made from multifilament nylon mesh, was ~ 2.2 m in length with an entrance aperture of 0.64 m^2. A collecting bag (50 cm long × 35 cm diameter), also of nylon mesh, was fastened to the rear end of the net by a heavy-duty zip-fastener. The sampling height was estimated from the elevation angle of the net (periodically measured with an inclinometer: ClinoMaster, Silva Ltd, Livingstone, UK) and from the length of tether paid out. At the end of each sample period the net was 'strangled' by means of a radio-controlled device, thus preventing contamination of the catch with low-flying fauna, before the blimp was winched down to ground level. The detachable net bag containing the catch was then removed from the net, and the organisms collected were killed with an insecticide (Dichlorvos 0.49 g per strip, Agrisense-BCS, Pontypridd, UK). A reading from a wind-run meter hung below the net was used to estimate the volume of air sampled in each period, and this was used to calculate the aerial density for each taxon caught (Riley *et al.*, 1995a).

To compare the relative abundance of different taxa in our results with the catches of the previous aerial trapping studies, logit-transformed percentages of the total catch were used. Because Hardy & Milne (1938) and Freeman (1945) only sampled during the daytime, comparison of our data with theirs has been restricted to daytime samples only. Patterns of diel periodicity in various taxa were analysed by comparing the mean aerial density of each group in each of the three main sampling periods: daytime (morning and afternoon combined), dusk and night-time. Due to the large numbers of zeroes in certain time periods, the data were not normal even after log transformation, and so were analysed with the non-parametric Kruskal-Wallis one-way ANOVA test in Genstat (version 6).

Results and Discussion

Composition of the aerial catches

In the 1999, 2000 and 2002 seasons, the number of aerial samples taken was 25, 36 and 36 respectively, totalling 132, 128 and 124 hours of sampling time. The numbers of specimens of various arthropod taxa caught are shown in full in appendix 1. Identifications to species were made more frequently in the 1999 catches than in the other years; hence many specimens not determined beyond family level in 2000 and 2002 may well be conspecific with individuals from the 1999 samples. The authors would be pleased to hear from any readers who might be interested in undertaking further identifications of particular taxa from the aerial netting collections.

The catches in the present study were compared with the catches from other high-altitude sampling programmes carried out in the UK, namely the kite netting samples taken at heights of 46–610 m by Hardy & Milne (1938) and the tower netting samples taken by Freeman (1945) at 54 m and 84 m above ground. Samples taken at Freeman's lowest height (3 m) were excluded, because much of the flight activity at that height may have been 'vegetative' (i.e. low-level local flights concerned with feeding and reproduction) rather than migratory. In addition, results from collections made by aerial netting from ships on the North Sea (Hardy & Milne, 1937; Hardy & Cheng, 1986) have been included, because these give a valuable indication of a species' capacity for prolonged flights. Table 1 shows our total catch ranked according to the numbers in each order compared with a similar ranking for the other studies, while fig. 1 shows the logit-transformed percentage of our total catch in each of the most abundant families plotted against the same figure for three of the other studies. It is clear that catches in the present study were broadly similar to those from the over-land studies of Hardy & Milne (1938) (fig. 1a, $r = 0.64$, $P < 0.05$) and Freeman (1945) (fig. 1b, $r = 0.77$, $P < 0.01$), and also to Hardy & Cheng's (1986) catches from over the North Sea (fig. 1c, $r = 0.69$, $P < 0.05$). Not surprisingly perhaps, the correlation between the data of Hardy & Milne (1938) and Freeman (1945), both from catches made during the 1930s over England was higher (fig. 1d, $r = 0.89$, $P < 0.001$) than that between our study and any of the others. Reasons for the similarities and differences between the studies are discussed for the major taxa below.

Hemiptera

Hemiptera were the most frequently represented order in our catches on account of the abundance of the aphids, of which 3344 were caught, representing 52% of all the arthropods in the samples (table 1). The dominance of the Aphididae in the airborne insect fauna over England is also apparent from the results of the other over-land netting studies (Hardy & Milne, 1938; Freeman, 1945) (table 1, fig. 1a,b). Over the North Sea, aphids were relegated to second place by 'acalyptrate Diptera' in the study of Hardy & Milne (1937), but in Hardy & Cheng's (1986) study, where samples were taken at least 80 km or 160 km from land, aphids were again the dominant group (table 1, fig. 1c). The cereal aphids *Sitobion avenae* (Fabricius) and *Rhopalosiphum padi* (Linnaeus) were by far the most common species in our samples, followed by *Myzus persicae* (Sulzer) (appendix 1). Movements of these aphid species in July would represent mid-season re-distributions between various summer hosts: e.g. *S. avenae* and *R. padi* would be emigrating from cereals onto wild grasses at this time (Taylor *et al*., 1982).

Considering the species composition of the 1930s aphid samples, it is noteworthy that the cabbage aphid, *Brevicoryne brassicae* Linnaeus, was very dominant in Freeman's (1945) study, followed by a *Myzus* sp. and *Brachycaudus helichrysi* (Kaltenbach) (referred to as *Anuraphis padi* Linnaeus). As these three species are brassica-feeders, their abundance may well have been due to the presence of market gardens in the vicinity of Freeman's sampling site. In Hardy & Milne's (1938) study, *B. helichrysi* was the most common aphid followed by *S. avenae* (referred to as *Macrosiphum granarium* Kirby). It is interesting to note, however, that in the collections made over the North Sea in summer 1938 (Hardy & Cheng, 1986) the cereal aphids *R. padi* and *S. avenae* were by far the most dominant species, as they were in the present study.

After the Aphididae, pysllids were next most numerous of the hemipteroid insects in our samples with 153 specimens captured, or 2.5% of all the insects. Pysllidae accounted for rather similar percentages in Hardy & Milne's (1938) and Freeman's (1945) catches (1.9% and 2.4% respectively) (fig. 1a,b). Psyllids comprised a much lower proportion of the North Sea catches (fig. 1c), indicating that this group is much less likely to make long distance flights compared to certain of the aphid species.

The Delphacidae were the third most common hemipteroid family in the present samples, and in the 1999 season at least the specimens were all *Javasella pellucida* (Fabricius). Several individuals of this species were trapped by Hardy & Milne (1938) at about 150 m, and a single specimen was caught far out in the North Sea by Hardy & Cheng (1986). *Javasella pellucida* has been extensively studied as it transmits several plant viruses and consequently is a serious pest of cereals, particularly in Scandinavia. References to its windborne movements can be found in Johnson (1969) and Denno & Perfect (1994); migration of macropterous morph adults facilitates the redistribution of different generations between various wild grasses and the alternative cultivated hosts in this wing-polymorphic polyphagous planthopper.

Diptera

The Diptera were generally the second most abundant order in the aerial netting studies both in and around the UK (table 1). They comprised 21% of all the arthropods taken in our samples, and about 20–30% in the other studies (except for that of Hardy & Milne (1937) where they comprised a much larger proportion (70%) of the catch) (table 1). The dipteran families frequently represented in all three of the over-land studies included: small Nematocera, particularly the Mycetophilidae and Sciaridae (fungus gnats), Cecidomyiidae (gall midges), Psychodidae (moth-flies) and Chironomidae (non-biting midges); two families from the Aschiza (viz. the Phoridae and Lonchopteridae); and certain families of the acalyptrate Schizophora (particularly the Ephydridae, Sphaeroceridae, Chloropidae and Agromyzidae). Another acalyptrate family, the Drosophilidae, was the most commonly represented dipteran family in the present study (appendix 1). In 1999, when species level identifications were made, 111 out of 115 drosophilids caught were *Scaptomyza pallida* (Zetterstedt), and it is likely that the majority of the drosophilids sampled in the other two years were also *S. pallida*. This species (referred to as *Scaptomyza disticha* Duda) was also very dominant in the collections of Hardy & Cheng (1986) from the middle of the North Sea (a total of 359 specimens,

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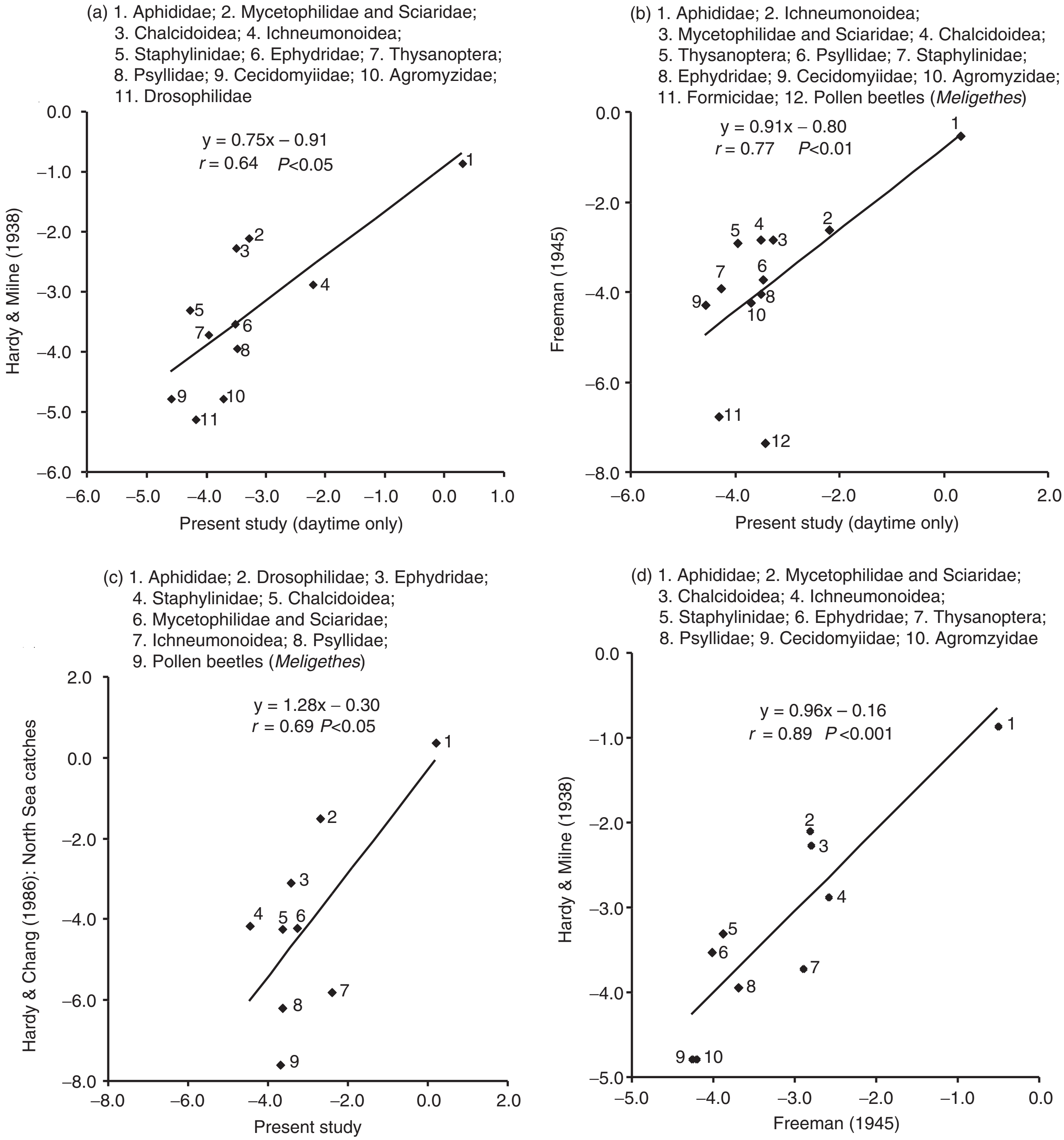

Fig. 1. A comparison of the relative abundance of different families (or hymenopteran superfamilies), shown as logit-transformed percentages of the total insect catch, in various aerial netting studies carried out over England or the North Sea: (a) present study versus Hardy & Milne (1938); (b) present study versus Freeman (1945); (c) present study versus Hardy & Cheng (1986); (d) Hardy & Milne (1938) versus Freeman (1945).

representing almost 60% of the Diptera caught), and it also comprised the majority of the 1351 drosophilids caught over the Pacific (Yoshimoto *et al.*, 1962, quoted in Johnson, 1969, p. 401). All this is evidence of high migratory flight endurance in some *S. pallida* individuals. Drosophilids were uncommon in the catches of Hardy & Milne (1938) (fig. 1a) and Freeman (1945), but the reasons for this are not clear.

The pest status of the chloropid species, *Oscinella frit* Linnaeus, has led to detailed investigations of its high-altitude migration in the UK (Johnson *et al.*, 1962), which have provided quantitative information on its flight periodicity, density-height profiles, and area densities of the migrants on landing. Johnson *et al.* (1962) estimated that the median height of flight was 400 m between 11.00 and 12.00;

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Table 1. Comparison of catches obtained during the present aerial netting study at ~200 m above Cardington airfield, Bedfordshire, UK with previous aerial trapping studies over England and the North Sea.

Study reference	Present study		Freeman, 1945				Hardy & Milne, 1938		Hardy & Milne, 1937		Hardy & Cheng, 1986	
Sampling location	Bedfordshire		Grimsby				Hull, Suffolk and Kent		North Sea		North Sea	
Year(s)	1999, 2000, 2002		1934, 1935				1932–1935		1936		1938	
Sampling period	July		March–November				April–October		August		June–October	
Time of sampling	Day and night		Day only				Day only		Day and night		Day and night	
Height of sampling	c. 200 m		84 m		54 m		546–610 m		12 m. or 60–120 m		Foremast head	
Order	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%
Hemiptera	3561	55.41	1423	48.16	1907	39.79	300	35.76	172	23.56	1167[a]	59.91
(Aphididae)	(3344)	(52.17)	(1223)	(41.39)	(1677)	(34.99)	(250)	(29.80)	(171)	(23.42)	(1158)	(38.82)
Diptera	1370	21.32	611	20.68	1215	25.35	278	33.13	514	70.41	602[b]	30.90
Hymenoptera	755	11.75	448	15.16	757	15.79	176	20.98	12	1.64	35	1.80
Coleoptera	319	4.96	183	6.19	345	7.20	57	6.79	0	0.00	38	1.95
Aranea	298	4.64	–		–		1	0.12	6	0.82	2	0.10
Thysanoptera	96	1.49	145	4.91	292	6.09	20	2.38	0	0.00	0	0.00
Psocoptera	17	0.26	138	4.67	269	5.61	5	0.60	0	0.00	1	0.05
Neuroptera	6	0.09	0	0.00	0	0.00	1	0.12	3	0.41	7	0.36
Lepidoptera	4	0.06	?		?		1	0.12	6	0.82	61	3.13
Orthoptera	1	0.02	0	0.00	0	0.00	0	0.00	0	0.00	0	0
Trichoptera	0	0.00	0	0.00	0	0.00	0	0.00	1	0.14	0	0
Others	0	0.00	7	0.24	8	0.17	0	0.00	0	0.00	35[c]	1.80
Unrecognizable									16	2.19		
Total	6427	100.00	2955	100.00	4793	100.00	839	100.00	730	100.00	1948[d]	100.00

Notes on Hardy & Cheng (1986):
[a]The number of Hemiptera was obtained from the number of Aphididae given in table 2 of Hardy & Cheng (1986) plus another 9 Hemiptera listed in their table 3.
[b]There is a discrepancy between the number of Diptera given in table 2 of Hardy & Cheng (1986) and the numbers listed in their table 3. Following the advice of Dr L. Cheng (personal communication) the larger number (602) derived from their table 3 was used in the present table.
[c]The number of 'Other' insects was obtained by reducing the number of 45 given in their table 2, by the 9 non-aphid Hemiptera (mentioned above) plus a single pscopteran (see their table 3) .
[d]The total number of arthropods caught includes the additional Diptera mentioned in (b) above.

that the average duration of flight was a little over 1 hour; and average movement during that time would have been about 24–32 km in the winds experienced by the flies. Some of these findings may well be applicable to other small day-flying Diptera which use the convective circulation of the air to disperse.

Taken together, the dipteran families listed above are often important constituents of the aerial fauna in other regions of the world. For example, in the extensive catches of insects over the oceans made by Gressitt, Yoshimoto and their co-workers, the families most abundantly represented were Drosophilidae, Chironomidae, Agromyzidae, Ceratopogonidae and Ephydridae (see summaries in table 1 of Holzapfel & Harrell, 1968; and table 5.3 of Bowden & Johnson, 1976), while in the day-time catches made from aircraft over the southern USA (Glick, 1939) the leading families were Chloropidae, Ephydridae, Chironomidae, Sphaeroceridae and Sciaridae (summary in Johnson, 1969, p. 300).

Hymenoptera

The third most abundant order in the aerial catches was the Hymenoptera (table 1), and in particular small-sized members of the superfamilies Ichneumonoidea or Chalcidoidea (fig. 1a). In our samples, 497 ichneumonoids and 153 chalcidoids were caught, accounting for 8.1% and 2.5% of the total insect catch, respectively. The equivalent percentages in Freeman's (1945) study were rather similar (7.0% and 5.4% respectively) (fig. 1b), but in Hardy & Milne's (1938) data the Chalcidoidea were more abundant (accounting for 9.4%) (fig.1a). In the catches made over the North Sea (fig. 1c), the Ichneumonoidea comprised a much lower proportion of the total catch than was the case over land, which may indicate lower powers of flight endurance compared to, say, the aphids or the Diptera families mentioned above. Ants (Formicidae) comprised the next most abundant group of hymenopterans in our samples, but nearly all of the 62 individuals were male *Lasius niger* (Linnaeus) taken on one afternoon (26 July 2002), when there was a large exodus of reproductives of this species in the vicinity of the sampling site. The comparatively high abundance of ants in the present study was presumably a stochastic event due to a local emergence, thus explaining the disparity between our data and that of the other studies.

Coleoptera

Coleoptera formed the fourth most abundant order in our catches (table 1), with Nitulidae (pollen beetles) and Staphylinidae the most abundant families (fig. 1a). The latter family was also a major constituent of the coleopteran fauna sampled at high-altitude over the UK (Hardy & Milne, 1938; Freeman, 1945) and over Louisiana (Glick, 1939). In the collections made over water, the Staphylinidae again predominated, both over the North Sea (Hardy & Cheng, 1986) and over the Pacific and other oceans sampled by Gressitt, Yoshimoto and others (see summaries in Holzapfel & Harrell, 1968; Bowden & Johnson, 1976).

The Nitidulidae in our catches were pollen beetles of the genus *Meligethes*, and were probably mostly *M. aeneus* (Fabricius). The adults of this species are known to make mass windborne migrations in July from winter-sown to spring-sown oilseed rape (Kenward, 1984; Mauchline, 2003), and our results indicate that they make use of high-altitude winds to do so. Pollen beetles were rare or absent in the previous trapping studies over England (fig. 1a,b), but were nonetheless caught over the North Sea by Hardy & Cheng (1986) (fig. 1c), indicating that long-distance flight is common in this group. The increased abundance of *Meligethes* spp. in the current study compared to the earlier studies may well be due to the greater prevalence of oilseed rape crops in recent decades.

Notes on species of special interest

In this section attention is drawn to some of the species caught by us at high-altitude that are of interest because they are either important pests or biocontrol agents, or are rare in the UK, or they are large enough to be detected by entomological radar. Large insects are usually so sparse in the air compared to small ones (e.g. the aerial density of a common noctuid moth may well be three orders of magnitude less than that of a common aphid; Johnson, 1969), that the capture of just one specimen of a large-sized insect in the aerial net is notable, and may well be indicative of a significant migration rate in the species concerned.

Pests and natural enemies

Aside from some of the aphid species caught (appendix 1) the most important crop pest recorded in the present study was the diamondback moth *Plutella xylostella* (Linnaeus) (Lepidoptera: Yponomeutidae). This species is a well known migrant, and it is presumed that UK populations are largely re-established each year by immigration from continental Europe (French & White, 1960). Evidence for the ability of *P. xylostella* to reach the UK via a sea-crossing include the large numbers (59 individuals) caught migrating across the North Sea by Hardy & Cheng (1986) and the arrival of many millions on the east coast of the UK in 1958 (French & White, 1960). Indeed, a study using VLR and flight trajectory analysis showed how windborne migration from continental Europe established the UK population in 2000 (Chapman *et al*., 2002). However, the primary immigration responsible for the establishment occurred in May 2000, and the three individuals trapped at 200 m in July of that year were part of a redistribution of locally-emerged adults of the second or third generation (Chapman *et al*., 2002).

Entomological radar studies are also being made on the high-altitude migration of three important groups of aphid predators – lacewings (Neuroptera: Chrysopidae and Hemerobiidae), hoverflies (Diptera: Syrphidae), and ladybirds (Coleoptera: Coccinellidae); and one group of important generalist predators – ground beetles (Coleoptera: Carabidae). Representatives of all of these taxa were caught in the aerial net during the present study (appendix 1), and one of the carabids, *Notiophilus biguttatus* (Fabricius), was amongst the most abundant of the larger species (> 5 mg) recorded (appendix 1). Two species of brown lacewings caught by us, namely *Hererobius humulinus* Linnaeus and *H. lutescens* Fabricius, appear to be capable of long flights as they were also taken over the North Sea by Hardy & Cheng (1986). The most important lacewing predator of aphids, the *Chrysoperla carnea* species complex, were not caught in the present study, but were present in aerial samples taken later in the season (late August) in 2003 (J.W. Chapman & D.R. Reynolds, unpublished data). The temporal patterns, behavioural strategies and pest-management implications of long-range windborne migration in all these groups of economically-important biocontrol agents are currently being investigated (Chapman *et al*., 2004).

Rare species

The large leaf-hopper *Athysanus argentarius* Metcalf (Hemiptera: Cicadellidae) has a very limited distribution in south-eastern England; until recently it was restricted to coastal and estuarine marshes and was thought to have limited flight ability (Salmon & Chapman, 2000). Thus the capture of this species over Bedfordshire in a day-time sample in 1999 was extraordinary, and is presumably linked to its recent spread to rank vegetation and damp grassland in various inland locations (Salmon & Chapman, 2000).

Phorid flies are quite frequently taken at altitude over Britain – both Freeman (1945) and Hardy & Milne (1938) caught a number of *Megaselia* spp., but among the Phoridae caught in the present study (appendix 1) was the first British record of an otherwise uncommon northern European species, *Triphleba renidens* Schmitz (Disney & Chapman, 2001).

Large species

The capture of a male lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer) (Orthoptera: Acrididae), weighing 75 mg, during a daytime sample at 200 m in 2002 is one of the most surprising results of the present study. The opinion of earlier authors was that European grasshoppers very seldom fly spontaneously (except for a few which make mating display flights) (Richards & Waloff, 1954; Uvarov, 1977), but more recent opinion is that males of *C. albomarginatus* fly readily (Marshall & Haes, 1988). This species is restricted to southern and eastern UK, and usually inhabits moist habitats such as salt-marshes and water meadows (Marshall & Haes, 1988). In recent decades *C. albomarginatus* has increased its range (Haes & Harding, 1997), possibly by utilizing farmland set-aside (Gardiner & Hill, 2003); presumably its range-expansion would be greatly facilitated by its ability to undergo long-range windborne dispersal. Although high-altitude flight by grasshoppers has been well documented in warmer regions of the world, e.g. southern USA (Glick, 1939), Sudan (Schaefer, 1976) and Mali (Reynolds & Riley, 1988), to our knowledge this specimen is the first acridoid to be caught migrating at high-altitude in Europe.

In many insect taxa there is a positive correlation between the degree of impermanence of the habitat and the level of migration (Southwood, 1962); thus it is not surprising that species inhabiting temporary ponds were caught in the balloon-supported net. The dytiscid diving beetle *Colymbetes fuscus* (Linnaeus), at 160 mg the largest beetle species trapped in the present study, is known to fly from temporary pools as they dry in the summer (Carr, 1989) and it frequently invades small artificial water pools by flight (Jackson, 1952). Dytiscids were sampled at high-altitude by Glick (1939), but this is the first European record of high-altitude windborne migration in the Dytiscidae. The smaller day-flying hydrophilid beetles in the genus *Helophorus* have been sampled at high-altitude in previous studies (Hardy & Milne, 1938; Glick, 1939; Freeman, 1945); those captures, and our records of *H. longitarsis* Wollaston, *C. fuscus*, and the corixid water boatman *Sigara distincta* (Fieber) (appendix 1), demonstrate that the colonization of new habitats by water beetles and bugs is facilitated by windborne movements high in the air and not just by flights at low altitudes.

The largest specimen caught in our aerial net was a large yellow underwing moth *Noctua pronuba* Linnaeus (Lepidoptera: Noctuidae), weighing 390 mg, caught at 150 m on the night of 16–17 July 1999. This species is a probable immigrant to the UK (Howard, 1999), but also an abundant resident, and thus it is often difficult to ascertain the origin of sudden increases in local populations. The winds were from the west when our *N. pronuba* was caught, and so a continental origin is not likely in this particular case. However, the displacement speeds often achieved by wind-assisted migrants at this altitude clearly demonstrate that on other occasions this species would be capable of immigration from continental Europe within a single night's flight period (cf. Chapman *et al*., 2002). A comprehensive suction trap survey of the height of flight of Macrolepidoptera in the UK did not find any noctuids (or other macro-moths) flying above 17 m (Taylor & Carter, 1961), and these groups were also absent from the aerial trapping results of Hardy & Milne (1938) and Freeman (1945). The present study indicates that UK night-time conditions are suitable for long-range windborne dispersal of noctuid moths at high altitude, at least on certain occasions.

Large insect targets (> 100 mg) are regularly recorded during the day and night by our entomological radar (Smith *et al*., 2000), and windborne migrations by the species mentioned above, or similar taxa, may well account for many of these large radar-detected individuals.

Diel periodicity

In 1964, Lewis & Taylor published a monumental study of diel flight periodicity in about 400 taxa of British insects, based on sampling near the ground with time-segregating suction traps. Lewis & Taylor regarded their catches as 'representing the ground level populations from which came the migrants represented by the samples of Hardy & Milne and Freeman' (and by the same token, the samples in the present study). However, it seems likely that some of the taxa caught in Lewis & Taylor's (1964) study were engaged in 'vegetative' flights rather than migration. In contrast, vegetative flights can be ruled out for the insects caught at our sampling height of 200 m. This is particularly so in view of the > 3 m s^{-1} wind speed needed for the net to sample properly – a speed in excess of the flight speeds of the small insects in the collections – which would prevent any insects (e.g. flies visually attracted to the balloon) from flying up- or cross-wind and congregating in the vicinity of the net. We thus consider the insects in our samples to have been engaged in migratory flight when they were captured, but comparison with Lewis & Taylor's (1964) low-altitude suction trapping results may be instructive as the latter should indicate possible times of take-off and emigration of species ascending to higher altitudes.

The mean aerial densities (estimated from all three seasons' samples) found during the day, dusk and night periods respectively, are shown in fig. 2 for nine abundant families (or hymenopteran superfamilies). Several diel patterns of migratory flight are distinguishable, although

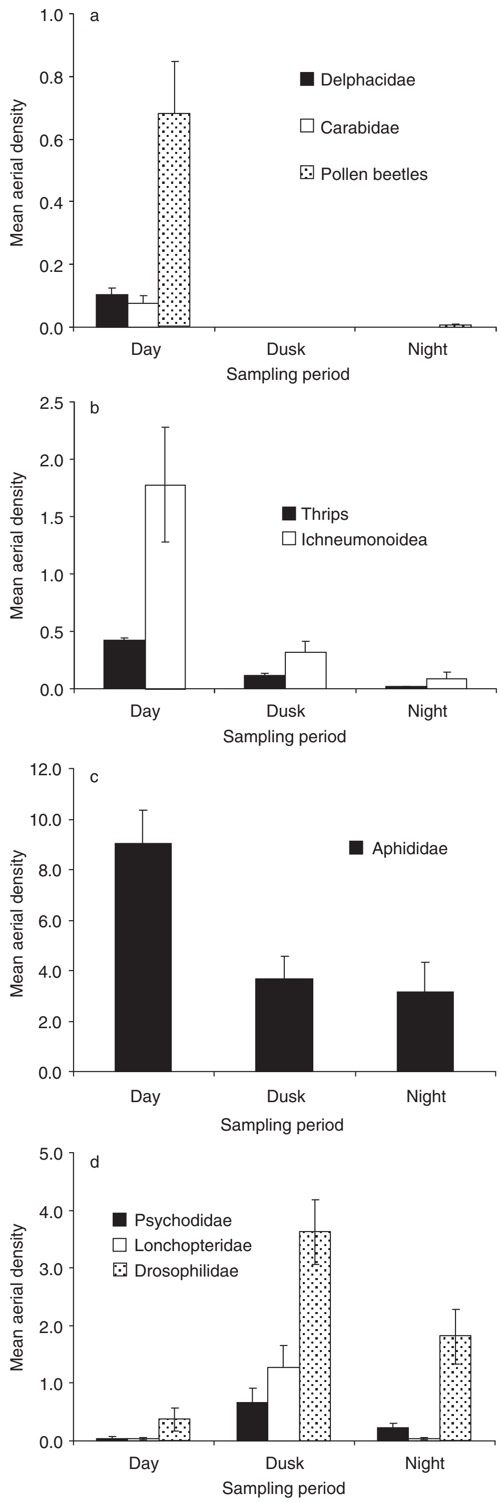

Fig. 2. Mean (± 1 SE) aerial density (numbers per 10^4 m^3) of selected common families (or hymenopteran superfamilies) caught during the day (10:00 – 18:00 BST), dusk (21:00 – 22:00 BST) or night (22:00 – 05:00 BST) sampling periods ~ 200 m above Cardington airfield, Bedfordshire, UK: (a) taxa with day-time emigration; (b) taxa exhibiting mainly day-time emigration, but with some flight during the night; (c) Aphididae; (d) dipteran families exhibiting mainly dusk, or dusk and dawn emigration.

variability between different species within a family may obscure patterns in some cases.

Day-time emigration

Some families were strongly day-flying, e.g. delphacid planthoppers (mostly *J. pellucida*), carabid beetles (mostly *N. biguttatus*) and nitidulid pollen beetles (*Meligethes* spp.) Activity was effectively limited to the day-time period in these three taxa (fig. 2a) and the effect of sampling period on aerial density was significant in all cases (Kruskal-Wallis tests; delphacids: H = 21.7, df = 2, P < 0.001; carabids: H = 11.3, df = 2, P < 0.01; pollen beetles: H = 38.5, df = 2, P < 0.001). *Meligethes* spp. beetles are known to have a normally distributed pattern of flight activity around noon in July (Lewis & Taylor, 1964, p. 450), and this agrees with the timing derived from the present catches at 200 m where only one individual out of 148 was taken outside of the daytime sampling periods.

Other groups were principally day active, but with occasional stragglers still airborne into the dusk period or beyond, for example thrips and Ichneumonoidea (fig. 2b). Their largely daytime flight resulted in a highly significant effect of time-period on activity (Kruskal-Wallis tests; thrips: H = 17.1, df = 2, P < 0.001; Ichneumonoidea: H = 38.2, df = 2, P < 0.001). This pattern graded into another, shown in the aphids (fig. 2c), where migratory activity started during the day, but with considerable numbers of individuals continuing in flight after dark on some occasions. For example, on 8 July 1999, a sample beginning later than usual (at 00.30h) demonstrated that quite a high density of aphids (25 per 10^4 m^3), largely of the commonest species *R. padi* and *S. avenae*, were in flight until after midnight. However, even though substantial densities were recorded at night (fig. 2c), the very high aphid densities in the daytime produced a highly significant effect of time-period on activity (H = 21.7, df = 2, P < 0.001).

The high-altitude migration of aphids has been the subject of very detailed quantitative studies in the UK, particularly by C.G. Johnson and L.R. Taylor (see references in Johnson, 1969). The present findings are not seriously at variance with the views of Johnson and Taylor, but continued aphid migration in the first few hours after darkness may be more common in the mid-summer months in the UK (as on 8 July 1999) than the impression given in some of their writings. Sometimes, for example, it is implied that the aphids land by nightfall and 'the upper air over southern England becomes almost clear at night' (Johnson, 1969, p. 344). On the other hand, sometimes it is said that the aphid populations declines at night and the air is clear by early morning (Johnson, 1951) – a statement with which the present authors would agree.

The persistence in flight of high densities of aphids after midnight, similar to the situation in warmer regions of the world (e.g. Berry and Taylor, 1968; Riley *et al*., 1995a), is no doubt the exception rather than the rule in southern UK, but these occasions are important because they can greatly increase the migratory ambit of the aphid. If night temperatures are suitable, flight may be especially prolonged under these circumstances compared to the durations (< 4 h) of daytime 'cumuliform' migratory flight (Taylor, 1986) because, in the dark, the migrant is effectively cut off from visual stimuli (e.g. of ground vegetation) which would tend to promote descent and

https://doi.org/10.1079/BER2004287 Published online by Cambridge University Press

landing. In addition, if a surface temperature inversion has developed, the migrant may be inhibited from descent into the layer of colder air near the ground. There was in fact evidence of an inversion on the above-mentioned night of 8 July 1999, with the maximum air temperature occurring near the aerial netting height (the midnight radiosonde at Herstmonceaux, East Sussex, for example, revealed temperatures of over 20°C at 120 and 240 m, as opposed to 17.8°C at the ground). Winds at the netting height were not particularly strong on this night, but on occasions where a low-level jet forms at the top of the night-time inversion (Taylor, 1986; Drake & Farrow, 1988) insect movements can be very rapid.

Dusk emigration

In contrast to day-flyers, night-flying groups took off around dusk and flight continued to a greater or lesser extent into the night. This pattern was shown by several families of Diptera, including the Psychodidae and Lonchopteridae (fig. 2d). Previous low-altitude studies indicate that the Pyschodidae show an activity profile that gradually reaches a maximum during the evening and then quickly declines (Lewis & Taylor, 1964). However, the present results show that while psychodid high-altitude migration was most common around dusk, it continued to a certain extent later into the night, i.e. after 22:00 h (fig. 2d) and on at least one occasion, after 00:15 h. However, there was very little flight in the daytime, and as a result the relationship between density and time was highly significant ($H = 13.8$, df = 2, $P < 0.001$). The capture of eight specimens of a *Pyschoda* sp. over the North Sea by Hardy & Cheng (1986) demonstrates that extended flights can occur in the Pyschodidae. Flight in the Lonchopteridae was almost entirely restricted to the short dusk period (fig. 2d), and consequently the effect of time-period on aerial density was highly significant ($H = 33.7$, df = 2, $P < 0.001$).

Dusk and dawn emigration

In the Drosophilidae, migration took place mainly in the evening twilight and the night, but it also occurred during the day (fig. 2d). As mentioned above, our drosophilid collections were dominated by *S. pallida*, and flight near ground level in this species has been well-documented by Lewis & Taylor (1964). They found that at Rothamsted in July, *S. pallida* (= *Drosophila disticha* (Duda)) showed a strong narrow peak of activity soon after sunset, and a much smaller peak after sunrise (see fig. 5e,f of Lewis & Taylor, 1964). Therefore our results are interpreted to mean that in summer the main emigration period of *S. pallida* was around dusk leading to night flight, but there was also some emigration in the early morning which could lead to lengthy daytime flights. However, the fact that flight was still concentrated in the dusk period, produced a highly significant effect of time-period on flight activity ($H = 31.6$, df = 2, $P < 0.001$). (It is interesting to note that crepuscular flight periodicities can be open to adaptive seasonal variation, particularly the movement of active peaks further into the daytime in the colder months: for example in October *S. pallida* has a flight pattern with a single broad peak around noon – as shown in fig. 10e,f of Lewis & Taylor, 1964.)

General discussion

Due to the practicalities, and the expense, of maintaining insect sampling platforms high in the air, this medium is usually the least studied of insect environments. There is thus the constant possibility that aerial movements will be ignored or insufficiently appreciated by ecologists and pest managers. Even when quite extensive studies of aerial populations have been made, 'the inchoate literature has not been satisfactorily systematised' (Bowden & Johnson, 1976). With this in mind, the present paper has outlined some results of a recent investigation of high-altitude insect movement over southern UK, and compared the results with those from studies made in the mid and late 1930s by Hardy & Milne (1937, 1938), Hardy & Cheng (1986) and Freeman (1945). Any conformity of results from studies carried out over 60 years apart, and at different sites, would seem to indicate that we are approaching definitive conclusions on the composition of the aerial fauna migrating at altitude over the southern UK, at least for the more abundant species.

Reference has been made above to some of the similarities between the present catches and those taken in the 1930s, e.g. with respect to the relative abundance of the Aphididae. Comparison of the abundances of individual species of aphids is more difficult – full species lists were not given by Freeman (1945), and there are differences of technique, seasonal timing and location between the studies. In fact, rigorous comparisons between years are probably only possible since the adoption of a standard sampling methodology for aphids (viz. the Rothamsted Insect Survey network of 12 m suction traps; Woiwod & Harrington, 1994), and data obtained by this means has only been available since the mid 1960s. Nonetheless, it is interesting to note that the most numerous species taken over land in the 1930s aerial samples, namely *Brevicoryne brassicae*, *Myzus* sp. and *Brachycaudus helichrysi*, were not graminaceous species, in contrast to the cereal aphids *Sitobion avenae* and *Rhopalosiphum padi* which were dominant in the present samples. This may be a reflection of the increasing areas devoted to large-scale cereal monoculture in eastern England since World War II.

On the other hand, in Hardy & Cheng's (1986) data collected in 1938 from far out over the North Sea, *S. avenae* and *R. padi* were very dominant, followed by *M. persicae* – exactly as in our samples. So, it appears that there has been little change since the 1930s in the aphid species with the potential to undertake long-range migrations. Rather similar sentiments apply to a handful of other species, e.g. the drosophilid fly *S. pallida*: they are certainly abundant in aerial samples taken over-land, but their dominance can increase hugely in over-water catches, due to their ability to make extended migrations.

The present work appears to be the first detailed report on high-altitude sampling over the UK, or elsewhere in Europe, at night: Hardy & Milne (1938) and Freeman (1945), in contrast, sampled only during daylight. The samples of Hardy & Milne (1937) and Hardy & Cheng (1986) from ships on the North Sea were continuous, day and night, but there is evidence that over-water flights can be atypically prolonged, at least in some insect species (Wolf *et al*., 1986), and thus the results are more indicative of a species' potential for very long flights, rather than demonstrating typical migratory flight periodicity. Investigation of high-altitude flight at night not only helps quantify the migration of insect taxa which take off at dusk, but draws attention to the occurrence of continuing flight after dark by some groups normally considered to be day-flying but which can maintain flight under low illumination levels as long as temperatures are suitable. Further increases in this phenomenon might be expected in the UK if global warming continues to produce a relative rise in minimum (night) temperatures (Houghton *et al*., 2001), thus ameliorating to a certain extent the considerable inhibitory effects of low night temperatures on nocturnal insect migrants in Britain.

Acknowledgements

The authors are grateful to the Director of the Meteorological Research Unit (UK Meteorological Office) for permission to operate the blimp within the official aircraft exclusion zone at Cardington, and thank David Bamber and other Met Office staff for their advice on various practical and administrative aspects of the balloon flying operations. Suzanne Dunn assisted with the balloon handling, and with the sorting of the aerial net samples. Advice on data analysis was provided by Suzanne Clark in the Rothamsted Research Biomathematics group, and Alice Mauchline supplied information on pollen beetle ecology. We also thank the following specialists for kindly agreeing to identify various insect taxa: Alison Haughton, Michael Salmon, Melissa Else, Colin Plant, David Manning, Mark Telfer, Jim Ashby, Patrick Roper, Adrian Plant, Henry Disney and Paul Beuk. Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council (BBSRC). This work was sponsored by BBSRC grant 206/D15558.

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Appendix 1

List of invertebrate taxa caught by aerial netting at ~ 200 m above Cardington airfield, Bedfordshire, UK, during July of 1999, 2000 and 2002.

Order	Family (or Superfamily)		Year			Total
			1999	2000	2002	
Orthoptera	Acrididae[1]	*Chorthippus albomarginatus* (De Geer)			1	1
Hemiptera	Anthocoridae[2]	*Anthocoris nemoralis* (Fabricius)		1		1
		Xylocoris galactinus (Fallén)		1		1
	Miridae	*Megaloceraea recticornis* (Geoffroy)[3]		2		2
		Orthops cervinus (Herrich-Schaeffer)[4]	1			1
		Orthotylus tenellus (Fallén)[2]			1	1
	Corixidae[2]	*Sigara distincta* (Fieber)		1		1
	Delphacidae[4]	*Javasella pellucida* (Fabricius)	17			17
		Unidentified Delphacidae		3	15	18
	Cicadellidae[4]	*Athysanus argentarius* Metcalf	1			1
		Deltocephalus pulicaris (Fallén)	2			2
		Psammotettix nodusus (Ribaut)	1			1
		Unidentified Cicadellidae		2	7	9
	Cercopidae[1]	*Philaenus spumarius* (Linnaeus)			1	1
	Aphididae[5]	*Acyrthosiphon pisum* (Harris)	45			45
		Anuraphis farfarae (Koch)	1			1
		Aphis fabae Scopoli	101			101
		Aphis salicariae Koch	40			40
		Aphis spp.	2			2
		Brachycaudus helichrysi (Kaltenbach)	3			3
		Brevicoryne brassicae (Linnaeus)	39			39
		Cavariella aegopodii (Scopoli)	1			1
		Cavariella pastinaceae (Linnaeus)	6			6
		Cavariella theobaldi (Gillette & Bragg)	1			1
		Cinara spp.	1			1
		Clethrobius comes (Walker)	1			1
		Eriosoma patchae (Börner & Blunck)	2			2
		Euceraphis punctipennis (Zetterstedt)	12			12
		Hyalopterus pruni (Geoffroy)	26			26
		Hyperomyzus latucae (Linnaeus)	5			5
		Macrosiphum euphorbiae (Thomas)	3			3
		Macrosiphum rosae (Linnaeus)	1			1
		Metopolophium dirhodum (Walker)	4			4
		Myzus cerasi (Fabricius)	7			7
		Myzus persicae (Sulzer)	272			272
		Pemphigus spp.	2			2
		Rhopalosiphum insertum (Walker)	19			19
		Rhopalosiphum maidis (Fitch)	1			1
		Rhopalosiphum nymphaeae (Linnaeus)	1			1
		Rhopalosiphum padi (Linnaeus)	737			737
		Sitobion avenae (Fabricius)	766			766
		Sitobion fragariae (Walker)	11			11
		Tuberculatus annulatus (Hartig)	2			2
		Uromelan spp.	1			1
		Utamphorophora humboldti (Essig)	1			1
		Unidentified Aphididae	22	673	535	1230
	Psyllidae[1]		18	33	102	153
	Unidentified Hemiptera			8		8

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Order	Family (or Superfamily)		Year			Total
			1999	2000	2002	
Psocoptera[1]	Caeciliidae	*Caecilius flavidus* (Stephens)			15	15
	Ectopsocidae				1	1
	Elipsocidae				1	1
Thysanoptera[1]	Thripidae	Mainly *Limothrips cerealium* Halliday	11	29	56	96
Neuroptera	Hemerobiidae[1]	*Hemerobius humulinus* Linnaeus	1	1		2
		Hemerobius lutescens Fabricius		1		1
		Wesmaelius nervosus (Fabricius)		1		1
		Micromus variegatus (Fabricius)			1	1
	Chrysopidae[6]	*Nineta flava* (Scopoli)	1			1
Lepidoptera	Yponomeutidae[7]	*Plutella xylostella* (Linnaeus)		3		3
	Noctuidae[1]	*Noctua pronuba* Linnaeus	1			1
Coleoptera	Carabidae[8]	*Notiophilus biguttatus* (Fabricius)	1	2	10	13
		Loricera pilicornis Fabricius		1	2	3
		Amara familaris Duftschmid		1	1	2
		Bembidion guttula Fabricius			1	1
		Bembidion articulatum Panzer			1	1
	Dytiscidae[1]	*Colymbetes fuscus* (Linnaeus)		1		1
	Hydrophilidae[9]	*Helophorus longitarsis* Wollaston		1		1
	Staphylinidae[9]	*Tachyporus hypnorum* (Fabricius)	1			1
		Unidentified Staphylinidae		14	54	68
	Cantharidae[9]	*Cantharis lateralis* Linnaeus	1			1
	Nitidulidae[9]	*Meligethes* spp., mostly *M. aeneus* (Fabricius)	15	41	92	148
	Coccinellidae[1]	*Adalia 2-punctata* (Linnaeus)			1	1
		Adalia 10-punctata (Linnaeus)			2	2
		Coccinella 7-punctata (Linnaeus)			3	3
		Propylea 14-punctata (Linnaeus)			1	1
	Cryptophagidae[1]			2		2
	Lathrididae[1]			4		4
	Phalacridae[1]	*Stilbus* sp.		1		1
	Chrysomelidae[1]		21	10	4	35
	Curculionidae[9]	*Ceutorhynchus quadridens* (Panzer)	1			1
		Unidentified Curculionidae		1	9	10
	Apionidae[1]			1		1
	Unidentified Coleoptera		2		16	18
Diptera	Limoniidae[10]	*Dicranomyia modesta* (Meigen)	2			2
		Unidentified Limoniidae		1	1	2
	Anisopodidae[10]	*Sylvicola punctatus* (Fabricius)	2			2
	Mycetophilidae/Sciaridae[10]	*Bradysia* spp.	6			6
		Mycetophila luctuosa Meigen	1			1
		Sciara sp.	2			2
		Unidentified Mycetophilidae/Sciaridae	6	55	149	210
	Cecidomyiidae[10]	*Lestremia cinerea* Macquart	2			2
		Unidentified Cecidomyiidae	23	66	63	152
	Psychodidae[10]	*Psychoda trinodulosa* Tonnoir	1			1
		Pyschoda phalaenoides (Linnaeus)	1			1
		Unidentified Psychodidae		33	22	55
	Scatopsidae[1]				2	2
	Culicidae[1]			1		1
	Ceratopogonidae[10]	*Culicoides pulicaris* (Linnaeus)	1			1
		Unidentified Ceratopogonidae		2	1	3
	Chironomidae[10]	*Microtendipes* sp.	1			1
		Smittia pratorum (Goetghebuer)	1			1
		Tanytarsini sp.	2			2
		Unidentified Chironomidae	1	1	1	3
	Hybotidae[11]	*Platypalpus longiseta* (Zetterstedt)	12	4	9	25
	Dolichopodidae[1]				1	1
	Phoridae[12]	*Borophaga subsultans* (Linnaeus)			1	1
		Diplonevra funebris (Meigen)			1	1
		Megaselia brevicostalis (Wood)			2	2
		Megaselia ciliata (Zetterstedt)			2	2
		Megaselia longicostalis (Wood)	1		1	2

Order	Family (or Superfamily)		Year			Total
			1999	2000	2002	
		Megaselia paludosa (Wood)			3	3
		Megaselia pleuralis (Wood)	1			1
		Megaselia pusilla (Meigen)			3	3
		Megaselia sp.	1		1	2
		Triphleba nudipalpis (Becker)			2	2
		Triphleba renidens Schmitz	1			1
		Unidentified Phoridae		3		3
	Lonchopteridae[10]	*Lonchoptera bifurcata* (Fallén)	2			2
		Lonchoptera lutea Panzer	8			8
		Unidentified Lonchopteridae		17	19	36
	Syrphidae[1]	*Episyrphus balteatus* (De Geer)	1			1
	Pallopteridae[1]				7	7
	Ulidiidae[1]	*Homalocephala* sp.		1		1
	Sepsidae[10]	*Sepsis cynipsea* (Linnaeus)	2			2
		Sepsis fulgens Meigen	2			2
		Unidentified Sepsidae		1	1	2
	Heleomyzidae[1]			1		1
	Sphaeroceridae[10]	*Pullimosina pullula* (Zetterstedt)	1			1
		Pteremis fenestralis (Fallén)	1			1
		Unidentified Sphaeroceridae		17	40	57
	Asteiidae[10]	*Asteia amoena* Meigen	1			1
	Ephydridae[1]		55	98	37	190
	Drosophilidae[13]	*Drosophila andalusiaca* Strobl	4			4
		Scaptomyza pallida (Zetterstedt)	111			111
		Unidentified Drosophilidae		154	108	262
	Agromyzidae[1]		19	80	22	121
	Anthomyzidae[1]				1	1
	Chloropidae[1]		1	13	25	39
	Anthomyiidae[1]		1	1		2
	Muscidae[1]			1		1
	Unidentified Diptera		12	5	1	18
Hymenoptera[1]	Ichneumonoidea		235	137	125	497
	Cynipoidea		10	4	11	25
	Chalcidoidea		19	18	116	153
	Proctotrupoidea		1	3	14	18
	Formicidae	*Lasius niger* (Linnaeus)			62	62
Araneae[1]			35	48	215	298
Total			2821	1604	2002	6427

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(Accepted 17 February 2003)

https://doi.org/10.1079/BER2004287 Published online by Cambridge University Press